

Output stream of inhibitory neuron with delayed feedback is non-Markovian

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Abstract

The instantaneous state of a neural network consists of both the degree of excitation of each neuron the network is composed of and positions of impulses in communication lines between the neurons. In neurophysiological experiments, the neuronal firing moments are registered, but not the state of communication lines. But future spiking moments depend essentially on the past positions of impulses in the lines. This suggests, that the sequence of intervals between firing moments (inter-spike intervals, ISIs) in the network could be non-Markovian.

In this paper, we address this question for a simplest possible neural “net”, namely, a single inhibitory neuron with delayed feedback. The neuron receives excitatory input from the driving Poisson stream and inhibitory impulses from its own output through the feedback line. We obtain analytic expressions for conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$, which gives the probability to get an output ISI of duration t_{n+1} provided the previous $(n + 1)$ output ISIs had durations t_n, \dots, t_1, t_0 . It is proven exactly, that $P(t_{n+1} | t_n, \dots, t_1, t_0)$ does not reduce to $P(t_{n+1} | t_n, \dots, t_1)$ for any $n \geq 0$. This means that the output ISIs stream cannot be represented as a Markov chain of any finite order.

1 Introduction

In a neural network, the main component parts are neurons and inter-neuronal communication lines – axons [1]. These same units are the main ones in most types of artificial neural networks [2]. If so, then the instantaneous dynamical state of a network must include dynamical states of all the neurons and communication lines the network is composed of. The state of a neuron can be described as its degree of excitation. The state of a line consists of information of whether the line is empty or conducts an impulse. If it does conduct, then the state of the line can be described by the amount of time which is required for the impulse to reach the end of the line (time to live).

In neurophysiological experiments, the triggering (spiking, firing) moments of individual neurons but not the states of communication lines are registered. The sequence of intervals between the consecutive moments (inter-spike intervals, ISIs) is frequently considered as a renewal [3] or Markovian [4] stochastic process. For a renewal process, the consecutive ISIs are mutually statistically independent. Moreover, all statistical characteristics of a spike train must be

derivable from the single-ISI probability distribution. Additionally, those characteristics must be the same for a shuffled spike train, obtained by randomly reordering the ISIs, since shuffling does not change the single-ISI probability distribution. On the other hand, the experimentally obtained spike trains in auditory [5] and visual [6] sensory systems does not support the ISIs' mutual independence. This is revealed by calculating the correlation coefficient between the adjacent ISIs, which appeared to be nonzero for the experimental spike trains, while it must be zero for any renewal process. Also, such characteristics as Fano factor curve and firing rate distribution calculated for shuffled spike trains differ qualitatively from those obtained for the intact ones. These observations can be associated with memory effects in the ISI sequence which arise from an underlying non-renewal process. Recently [7], such a possibility was analyzed for weakly electric fish electrosensory afferents using high-order interval analysis, count analysis, and Markov-order analysis. The authors conclude that the experimental evidence cannot reject the null hypothesis that the underlying Markov chain model is of order m or higher, or maybe non-Markovian. The limited data sets used in [7] allow to establish a lower bound for m as $m \geq 7$ for some fibers.

What could be possible sources of such non-renewal, or even non-Markovian, behavior in real neural network? First, this behavior could be inherited from non-renewal (non-Markovian) character of the input signal. Second, intrinsic neuronal properties, such as adaptation, could be responsible. Finally, as we show here, the presence of delayed feedback interconnections itself could be the possible source of the non-Markovian behavior.

The non-Markovian behavior of the ISI sequence from neuron in a network with delayed interconnections is not surprising. Indeed, the information about which neurons are spiking/silent at any given moment of time leaves unknown the position of impulses in the interconnection lines at that moment. And it is the previous firing moments which determine the states of interconnection lines, which in turn determine the next firing moments. Therefore, information about the previous neuronal firing moments could improve our predicting ability as regards the next firing moments.

In this paper, we consider a simplest neural "net", namely, a single neuron with delayed feedback, which is driven with Poisson process. As neuronal model we take binding neuron as it allows rigorous mathematical treatment. We study the ISI output stream of this system and prove that it cannot be presented as Markovian chain of any finite order. This suggests that activity of any network with delayed interconnections, if presented in terms of neuronal firing moments, should be non-Markovian as well.

2 The object under consideration

2.1 Binding neuron model

The understanding of mechanisms of higher brain functions expects a continuous reduction from higher activities to lower ones, eventually, to activities in individual neurons, expressed in terms of membrane potentials and ionic currents. But the description of the higher brain functions in terms of potentials and currents in parts of individual neurons would be difficult, similarly as it

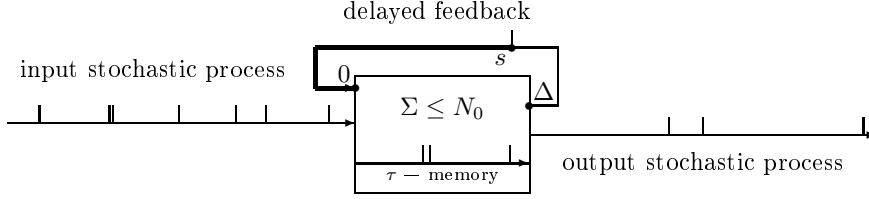


Figure 1: Binding neuron with feedback line under Poisson stimulation. Multiple input lines with Poisson streams are joined into a single one here. Δ is the delay duration in the feedback line.

would be difficult to describe execution of computer programs by a CPU in terms of Kirhgoff's laws. In this connection, it would be helpful to abstract from the rules by which a neuron changes its membrane potentials to rules by which the input impulse signals are processed in the neuron and determine its output firing activity. The coincidence detector, and temporal integrator are the examples of such an abstraction, see discussion in [9].

One more abstraction, the binding neuron (BN) model, is proposed as signal processing unit [10], which can operate either as coincidence detector, or temporal integrator, depending on quantitative characteristics of stimulation applied. This conforms with behavior of real neurons, see, e.g. [11, 12]. The BN model describes functioning of a neuron in terms of discrete events, which are input and output impulses, and degree of temporal coherence between the input events, see [8] for detailed description. Mathematically, this model can be realized as follows. We expect that all input impulses in all input lines are identical. Each input impulse is stored in the BN for a fixed time, τ . The τ is similar to the tolerance interval discussed in [13]. All input lines are excitatory. The neuron fires an output impulse if the number of stored impulses, Σ , is equal or higher than the threshold value, N_0 . After that, BN clears its memory and is ready to receive fresh inputs. That is, every input impulse either disappears contributing to a triggering event, or it is lost after spending τ units of time in the neuron's internal memory. The latter represents leakage. Here, the leakage is abrupt, while in more traditional models it is gradual.

The BN model is not general, but somewhat inspired by neurons as integrators up to a threshold. Its name is suggested by binding of features/events in large-scale neuronal circuits [14, 15, 16]. Its operational simplicity is provided by the fact that each input impulse traces entirely disappear after finite time τ . This is in the contrast to more familiar models where the traces (excitatory postsynaptic potentials, EPSP) decay exponentially. E. g., in the leaky integrate-and-fire model, EPSP is mimicked as pure exponential function the traces of which can disappear completely only after triggering. In the BN model, the EPSP is mimicked as box function of width/duration τ and the traces are stored in the neuron no longer than τ units of time.

Further, we expect that input stream in each input line is the Poisson one with some intensity λ_i . In this case, all input lines can be collapsed into a single one delivering Poisson stream of intensity $\lambda = \sum_i \lambda_i$, see Figure 1.

For analytic derivation, we use BN with $N_0 = 2$ in order to keep mathematical expressions shorter. It seems, that cases with higher thresholds might be considered with the same approach, but even $N_0 = 3$ without feedback requires

additional combinatorial efforts, see [17]. Therefore, cases of higher threshold are tested here only numerically.

As regards real biological neurons, the number of synaptic impulses in the internal memory which is necessary to trigger a neuron, varies from one [18], through fifty [19], to 60-180 [20], and 100-300 [21].

2.2 Feedback line action

In real neuronal systems, a neuron can form synapses from its axonal branch to its own dendritic tree [22, 23, 24, 25, 26, 27, 28, 29]. Synapses of this type are called autapses. Some of the neurons forming autapses are known to be inhibitory, see [24, 27, 28] for experimental evidence. As a result, the neuron stimulates itself obtaining an inhibitory impulse through an autapse after each firing with some propagation delay. We model this situation assuming that output impulses of BN are fed back into BN's input with delay Δ . This gives the inhibitory BN with delayed feedback model, Figure 1.

The inhibitory action of feedback impulses is modeled in the following way. When the inhibitory impulse reaches BN, it annihilates all excitatory impulses already present in the BN's memory, similarly as the Cl-type inhibition shunts depolarization of excitable membrane, see [31]. If at the moment of inhibitory impulse arrival, the neuron is empty, then the impulse disappears without any action, similarly as Cl-type inhibition does not affect membrane's voltage in its resting state. Such inhibition is "fast" in that sense, that the inhibitory impulses act instantaneously and are not remembered by neuron. This simple behavior is approved by relatively fast kinetics of the chloride inhibitory postsynaptic currents [32].

The feedback line either keeps one impulse, or keeps no impulses and cannot convey two or more impulses at the same time. Biological correlates supporting to an extent this assumption could be a prolonged refractory time and/or short-term synaptic depression. The latter can have the recovery time up to 20 s [30]. If the feedback line is empty at the moment of firing, the output impulse enters the line, and after time interval equal Δ reaches the BN's input. If the line already keeps one impulse at the moment of firing, the just fired impulse ignores the line.

This means, that at the beginning of an output ISI the feedback line is never empty. In order to describe the state of the feedback line, we introduce the stochastic variable s , $s \in [0; \Delta]$, which gives the time to live of the impulse in the feedback line, see Fig 1. Hereinafter, we will use the values of s just at the moments of output ISI beginnings (just after firings).

We assume, that time delay Δ of impulse in the feedback line is smaller than the BN's memory duration, τ :

$$\Delta < \tau. \quad (1)$$

It allows to make analytic expressions shorter. Also, the assumption (1) is consistent with the case of direct feedback, not mediated by other neurons.

3 Statement of the problem

The input stream of impulses, which drives neuronal activity is the Poisson stream. It is stochastic, therefore, the output activity of our system requires

probabilistic description in spite of the fact that both the BN and the feedback line action mechanisms are deterministic. We treat the output stream of inhibitory BN with delayed feedback as the stationary process¹. In order to describe its statistics, we introduce the following basic functions:

- the joint probability density $P(t_m, t_{m-1}, \dots, t_0)$ for $(m + 1)$ successive output ISI durations, t_0 is the first one.
- the conditional probability density $P(t_m | t_{m-1}, \dots, t_0)$ for output ISI durations; $P(t_m | t_{m-1}, \dots, t_0)dt_m$ gives the probability to obtain an output ISI of duration between t_m and $t_m + dt_m$ provided the previous m ISIs had durations $t_{m-1}, t_{m-2}, \dots, t_0$, respectively.

Definition 1. *The sequence of random variables $\{t_j\}$, taking values in Ω , is called the Markov chain of the order $n \geq 0$, if*

$$\forall_{m>n} \forall_{t_0 \in \Omega} \dots \forall_{t_m \in \Omega} P(t_m | t_{m-1}, \dots, t_0) = P(t_m | t_{m-1}, \dots, t_{m-n}),$$

and this equation does not hold for any $n' < n$ (see e.g. [33]). In the case of ISIs one reads $\Omega = \mathbb{R}^+$.

In particular, taking $m = n + 1$, we have the necessary condition

$$P(t_{n+1} | t_n, \dots, t_1, t_0) = P(t_{n+1} | t_n, \dots, t_1),$$

$$t_i \in \mathbb{R}^+, \quad i = 0, \dots, n + 1, \quad (2)$$

required for the stochastic process $\{t_j\}$ of ISIs to be the n -order Markov chain.

Our purpose in this paper is to prove the following theorem.

Theorem 1. *The output ISIs stream of inhibitory BN with delayed feedback under Poisson stimulation cannot be represented as a Markov chain of any finite order.*

4 Main calculations

This section with Appendices contains the required proof of Theorem 1.

4.1 Proof outline

In order to prove the Theorem 1, we are going to show analytically, that the equality (2) does not hold for any finite value of n . Namely, we will derive the exact analytic expression for the conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$ and show, that it depends on t_0 for any finite number n .

For this purpose we introduce the stream \mathbf{ts} of events (t, s)

$$\mathbf{ts} = \{\dots, (t_i, s_i), \dots\},$$

where s_i is the time to live of the impulse in the feedback line at the moment, when the ISI t_i starts. We consider the joint probability density $P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0)$

¹ The stationarity of the output stream results both from the stationarity of the input one and from the absence of time-dependent parameters in the BN model, see Section 2.1. In order to ensure stationarity, we also expect that system is considered after initial period sufficient to forget the initial conditions.

for realization of $(n + 2)$ successive events (t, s) , and the corresponding conditional probability density $P(t_{n+1}, s_{n+1} | t_n, s_n; \dots; t_0, s_0)$ for these events.

Then, we proof the following lemma, which will be used in our calculations.

Lemma 1. *Stream \mathbf{ts} is the 1-st order Markovian:*

$$\forall_{n \geq 0} \forall_{t_0 > 0} \forall_{s_0 \in]0; \Delta]} \dots \forall_{t_{n+1} > 0} \forall_{s_{n+1} \in]0; \Delta]} \\ P(t_{n+1}, s_{n+1} | t_n, s_n; \dots; t_0, s_0) = P(t_{n+1}, s_{n+1} | t_n, s_n), \quad (3)$$

where $\{t_0, \dots, t_{n+1}\}$ is the set of successive ISIs, and $\{s_0, \dots, s_{n+1}\}$ are the corresponding times to live.

See Appendix A for the proof.

Then, in order to find the conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$, we perform the following steps:

- *Step 1.* Use the property (3) for calculating joint probability density of events (t, s) :

$$P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0) = \\ P(t_{n+1}, s_{n+1} | t_n, s_n) \dots P(t_1, s_1 | t_0, s_0) P(t_0, s_0), \quad (4)$$

where $P(t, s)$ and $P(t_n, s_n | t_{n-1}, s_{n-1})$ denote the stationary probability density and conditional probability density (transition probability) for events (t, s) .

- *Step 2.* Represent $P(t_{n+1}, t_n, \dots, t_0)$ as marginal probability by integration over variables $s_i, i = 0, 1, \dots, n + 1$:

$$P(t_{n+1}, t_n, \dots, t_0) = \\ \int_0^\Delta ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0). \quad (5)$$

- *Step 3.* Use the definition of conditional probability density:

$$P(t_{n+1} | t_n, \dots, t_1, t_0) = \frac{P(t_{n+1}, t_n, \dots, t_0)}{P(t_n, \dots, t_0)}. \quad (6)$$

Taking into account the Steps 1 and 2, one derives for the joint probability density

$$P(t_{n+1}, t_n, \dots, t_0) = \\ \int_0^\Delta ds_0 \dots \int_0^\Delta ds_{n+1} P(t_0, s_0) \prod_{k=1}^{n+1} P(t_k, s_k | t_{k-1}, s_{k-1}). \quad (7)$$

In the next sections, we are going to find the exact analytic expressions for probability densities $P(t, s)$ and $P(t_k, s_k | t_{k-1}, s_{k-1})$, and perform the integration in (7). Then we will apply the Step 3, above, to find expressions for the conditional probability densities $P(t_{n+1} | t_n, \dots, t_0)$. It appears, that $P(t_{n+1} | t_n, \dots, t_0)$ is a function with jump discontinuities. In order to prove that the equality (2) does not hold for any $n \geq 0$, we analyze the positions of that jump discontinuities only.

4.2 Probability density $P(t, s)$ for events (t, s)

The probability density $P(t, s)$ can be derived as the product

$$P(t, s) = F(t | s)f(s), \quad (8)$$

where $f(s)$ denotes the stationary probability density for time to live of the impulse in the feedback line at the moment of an output ISI beginning, $F(t | s)$ denotes conditional probability density for ISI duration provided the time to live of the impulse in the feedback line equals s at the moment of this ISI beginning. Exact expressions for both $f(s)$ and $F(t | s)$ for inhibitory neuron with delayed feedback are calculated in [34]. Particularly,

$$F(t | s) = \begin{cases} \lambda^2 t e^{-\lambda t}, & t \in]0; s[, \\ (1 + \lambda s) e^{-\lambda s} P^0(t - s), & t \geq s, \end{cases} \quad (9)$$

where $P^0(t)$, $t > 0$, denotes an output ISI probability density for BN without feedback, which was obtained in [17, Eq. (3)]. Explicit expressions for $P^0(t)$ are different for different domains of t . For example,

$$P^0(t) = \lambda^2 t e^{-\lambda t}, \quad t \in]0; \tau]. \quad (10)$$

It is proven in [17], that $P^0(t)$ is a continuous function for whole range of ISI durations: $t \in]0; \infty[$.

It is essential for further study, that $F(t | s)$ considered as function of t has a jump discontinuity at $t = s$. Indeed, using (9) and (10), one obtains

$$\begin{aligned} \lim_{t \rightarrow s-0} F(t | s) &= \lambda^2 s e^{-\lambda s} > 0, \quad s \in]0; \Delta], \\ \lim_{t \rightarrow s+0} F(t | s) &= 0. \end{aligned}$$

The presence of jump in $F(t | s)$ at $t = s$ can be explained as follows. According to the definition of $F(t | s)$, the inhibitory impulse from the feedback line arrives s seconds later than the ISI t starts. After the inhibitory impulse arrival, it is guaranteed, that the BN is empty. To trigger the BN just after that moment, it is necessary to get two impulses from the input stream within infinitesimally small time interval. This event has infinitesimally small probability for the Poisson process (as well as for any other point process). That is why, the value of probability density $F(t | s)$ drops to zero at $t = s + 0$ and $F(t | s)$ experiences discontinuity at $t = s$.

It is important to emphasize, that $F(t | s)$ is a continuous function elsewhere except of the point $t = s$, where it has strictly positive jump. This follows from (9) and from the continuity of $P^0(t)$. The continuity of $F(t | s)$ at $t \in]0; s[$ and $t \in]s; \infty[$, and its jump at $t = s$ will be used later.

We also need an expression for $f(s)$, which is

$$f(s) = a \cdot \delta(s - \Delta) + g(s), \quad \text{where} \quad a = \frac{4e^{2\lambda\Delta}}{(3 + 2\lambda\Delta)e^{2\lambda\Delta} + 1}, \quad (11)$$

where $\delta(\cdot)$ – is the Dirac delta-function, $g(s)$ – is a regular function, which vanishes out of interval $s \in]0; \Delta]$ (see [34, Eq. (15)] for the exact expression),

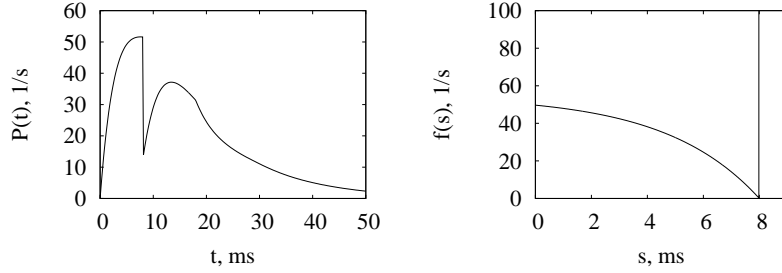


Figure 2: *Left*: output ISI probability density $P(t)$ reproduced from [34, Fig. 2]; *Right*: probability density $f(s)$ for times to live of the impulse in the feedback line. Here $\tau = 10$ ms, $\Delta = 8$ ms, $\lambda = 150$ s⁻¹, $N_0=2$.

the a gives the probability to obtain the impulse in the feedback line with time to live equal Δ at the beginning of an arbitrary output ISI, λ — is the input Poisson stream intensity.

Let us explain the presence of Dirac δ -function type singularity in $f(s)$. The probability to have time to live, s , exactly equal Δ at the moment of an output ISI beginning is not infinitesimally small. Every time, when the line is free at the moment of an output ISI beginning, the impulse enters the line and has time to live equal Δ . For the line to be free from impulses at the moment of triggering, it is necessary that $t > s$ for the previous ISI. The set of realizations of the input Poisson process, each realization satisfying $t > s$, has non-zero probability a , see (11), and this gives the δ -function at $s = \Delta$ in the probability density $f(s)$.

The output ISI probability density $P(t)$ for inhibitory neuron with delayed feedback can be obtained as the result of integration of (8):

$$P(t) = \int_0^\Delta F(t|s)f(s)ds. \quad (12)$$

Discontinuity of $F(t|s)$ at $t = s$ and δ -function type singularity at $s = \Delta$ in $f(s)$ result in discontinuity of $P(t)$ at $t = \Delta$.

Examples of $P(t)$ and $f(s)$ graphs can be found in Fig. 2.

4.3 Conditional probability density $P(t_k, s_k | t_{k-1}, s_{k-1})$

Here we find the conditional probability density $P(t_k, s_k | t_{k-1}, s_{k-1})$ for events (t_k, s_k) , which determines the probability to obtain the event (t_k, s_k) , with precision $dt_k ds_k$, provided the previous event was (t_{k-1}, s_{k-1}) . By definition of conditional probabilities, the probability density wanted can be represented as the following product

$$P(t_k, s_k | t_{k-1}, s_{k-1}) = F(t_k | s_k, t_{k-1}, s_{k-1})f(s_k | t_{k-1}, s_{k-1}), \quad (13)$$

where $F(t_k | s_k, t_{k-1}, s_{k-1})$ denotes conditional probability density for ISI duration, t_k , provided i) this ISI started with lifetime of impulse in the feedback line equal to s_k , and ii) previous (t, s) -event was (t_{k-1}, s_{k-1}) ; the $f(s_k | t_{k-1}, s_{k-1})$

denotes conditional probability density for times to live of impulse in the feedback line under condition ii). It is obvious, that

$$F(t_k | s_k, t_{k-1}, s_{k-1}) = F(t_k | s_k), \quad (14)$$

because with s_k being known, the previous event (t_{k-1}, s_{k-1}) does not add any information, useful to predict t_k (compare with the proof of Lemma 1, Appendix A).

In order to find the probability density $f(s_k | t_{k-1}, s_{k-1})$, let us consider various possible relations between t_{k-1} and s_{k-1} . If $t_{k-1} \geq s_{k-1}$, the line will have time to get free from the impulse during the ISI t_{k-1} . That is why at the beginning of the ISI t_k , an output spike will enter the line and will have time to live $s_k = \Delta$ with probability 1. Therefore, the probability density contains the corresponding δ -function:

$$f(s_k | t_{k-1}, s_{k-1}) = \delta(s_k - \Delta), \quad t_{k-1} \geq s_{k-1}. \quad (15)$$

If $t_{k-1} < s_{k-1}$, than the ISI t_{k-1} ends before the impulse leaves the feedback line. Therefore, at the beginning of the t_k , the line still keeps the same impulse as at the beginning of t_{k-1} . This impulse has time to live being equal to $s_k = s_{k-1} - t_{k-1}$, so

$$f(s_k | t_{k-1}, s_{k-1}) = \delta(s_k - s_{k-1} + t_{k-1}), \quad t_{k-1} < s_{k-1}. \quad (16)$$

Taking all together, for the conditional probability density $P(t_k, s_k | t_{k-1}, s_{k-1})$ one obtains

$$\begin{aligned} P(t_k, s_k | t_{k-1}, s_{k-1}) &= F(t_k | s_k) \delta(s_k - \Delta), & t_{k-1} \geq s_{k-1}, \\ &= F(t_k | s_k) \delta(s_k - s_{k-1} + t_{k-1}), & t_{k-1} < s_{k-1}, \end{aligned} \quad (17)$$

where exact expression for $F(t | s)$ is given in (9).

4.4 Joint probability density $P(t_{n+1}, \dots, t_0)$

In this section, we are going to find the exact analytic expression for the joint probability density $P(t_{n+1}, \dots, t_0)$ at the following domain

$$D_1 = \left\{ (t_0, \dots, t_n, t_{n+1}) \mid \sum_{i=0}^n t_i < \Delta \right\}. \quad (18)$$

Notice, that coordinate t_{n+1} is not included to the condition here. The set of $(n+2)$ successive ISI durations t_0, \dots, t_n, t_{n+1} has non-zero probability, $p_\Delta > 0$, to fall into the domain (18). Indeed, BN with threshold $N_0 = 2$ requires $2(n+1)$ input impulses within time window $]0; \Delta[$ to be triggered $(n+1)$ times within this window (condition (1) ensures that no one input impulse will be lost). BN receives excitatory impulses from the Poisson stream and inhibitory impulses from the feedback line. But no more than one impulse from the line may have time to reach BN's input during time interval less than Δ . Therefore, if as much as $(2n+3)$ input impulses are received from the Poisson stream during the time interval $]0; \Delta[$, the inequality (18) holds for sure, no matter was an impulse from the feedback line involved, or not. Therefore, $p_\Delta > p(2n+3, \Delta) > 0$, where

$p(i, \Delta)$ gives the probability to obtain i impulses from the Poisson stream during time interval Δ [35]: $p(i, \Delta) = e^{-\lambda\Delta}(\lambda\Delta)^i/i!$.

For a fixed $(n+2)$ -tuple $(t_0, \dots, t_n, t_{n+1}) \in D_1$, let us split the integration domain for s_0 in (7) in the following way:

$$]0; \Delta] =]0; t_0] \cup]t_0; t_0 + t_1] \cup]t_0 + t_1; t_0 + t_1 + t_2] \cup \dots \cup]t_0 + t_1 + \dots + t_n; \Delta],$$

or

$$\int_0^\Delta ds_0 = \int_0^{t_0} ds_0 + \sum_{i=1}^n \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} ds_0 + \int_{\sum_{j=0}^n t_j}^\Delta ds_0,$$

and introduce the following notations:

$$I_i = \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} P(t_0, s_0) \prod_{k=1}^{n+1} P(t_k, s_k \mid t_{k-1}, s_{k-1}),$$

$$i = 0, 1, 2, \dots, n, \quad (19)$$

$$I_{n+1} = \int_{\sum_{j=0}^n t_j}^\Delta ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} P(t_0, s_0) \prod_{k=1}^{n+1} P(t_k, s_k \mid t_{k-1}, s_{k-1}), \quad (20)$$

where we assume, that $\sum_{j=j_1}^{j_2} = 0$ for $j_1 > j_2$.

According to (7), (19) and (20), the probability density $P(t_{n+1}, \dots, t_0)$ can be obtained as

$$P(t_{n+1}, \dots, t_0) = \sum_{i=0}^{n+1} I_i. \quad (21)$$

Substituting $P(t_0, s_0)$ and $P(t_k, s_k \mid t_{k-1}, s_{k-1})$ from expressions (8) and (17) to (19) and (20) and performing integration over variables s_1, \dots, s_{n+1} , one obtains

$$I_i = \prod_{k=i+1}^{n+1} F(t_k \mid \Delta - \sum_{j=i+1}^{k-1} t_j) \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} \prod_{k=0}^i F(t_k \mid s_0 - \sum_{j=0}^{k-1} t_j) g(s_0) ds_0,$$

$$i = 0, 1, 2, \dots, n. \quad (22)$$

$$I_{n+1} = \int_{\sum_{j=0}^n t_j}^\Delta \prod_{k=0}^{n+1} F(t_k \mid s_0 - \sum_{j=0}^{k-1} t_j) g(s_0) ds_0 + a \prod_{k=0}^{n+1} F(t_k \mid \Delta - \sum_{j=0}^{k-1} t_j), \quad (23)$$

where $F(t \mid s)$ and $g(s)$ were defined in (9) and (11) (see Appendix B for the details of integration).

Taking into account (21), (22) and (23), one obtains the following expression for the joint probability density for output ISI durations:

$$\begin{aligned}
P(t_{n+1}, \dots, t_0) &= \sum_{i=0}^{n+1} I_i \\
&= \sum_{i=0}^n \prod_{k=i+1}^{n+1} F(t_k | \Delta - \sum_{j=i+1}^{k-1} t_j) \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} g(s_0) \prod_{k=0}^i F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) ds_0 \\
&\quad + \int_{\sum_{j=0}^n t_j}^{\Delta} g(s_0) \prod_{k=0}^{n+1} F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) ds_0 + a \prod_{k=0}^{n+1} F(t_k | \Delta - \sum_{j=0}^{k-1} t_j), \\
&\quad \sum_{i=0}^n t_i < \Delta, \quad n = 0, 1, \dots, \quad (24)
\end{aligned}$$

where we assume, that $\sum_{j=j_1}^{j_2} t_j = 0$ and $\prod_{j=j_1}^{j_2} F(t_j) = 1$ for $j_1 > j_2$.

The expression (24) gives the joint probability density $P(t_{n+1}, \dots, t_0)$ for consecutive ISI durations at the domain D_1 for an arbitrary n . Therefore, the conditional probability density $P(t_{n+1} | t_n, \dots, t_0)$ at D_1 can be obtained readily, see equation (6).

4.5 Discontinuities in $P(t_{n+1}, \dots, t_0)$

In this section, we will answer two following questions: i) does the $P(t_{n+1}, \dots, t_0)$ contain discontinuities at D_1 ? and ii) if it does, what are the positions of that discontinuities?

In order to ascertain the continuity of expression, defined in (24), let us first analyze the behavior of I_i , $i = 0, \dots, n$, and I_{n+1} separately.

Consider I_i , defined in (22). Since, at D_1 , $t_k < \Delta - \sum_{j=i+1}^{k-1} t_j$ for any $k = i+1, \dots, n$, the functions $F(t_k | \Delta - \sum_{j=i+1}^{k-1} t_j)$ are continuous, see (9). The factor $F(t_{n+1} | \Delta - \sum_{j=i+1}^n t_j)$ undergoes a nonzero jump discontinuity when point (t_0, \dots, t_{n+1}) transverses the hyperplane defined as

$$\sum_{j=i+1}^{n+1} t_j = \Delta, \quad i = 0, \dots, n, \quad (25)$$

and is continuous function anywhere else. The result of integration in (22) is a continuous function in D_1 , see the proof in Appendix C. Therefore, at the domain D_1 , each I_i has a discontinuity of a jump type at the hyperplane defined in (25).

Now, consider the continuity of I_{n+1} , expression (23). The first term, again, is a continuous function in D_1 , the proof is similar to what is done in Appendix C. The only discontinuity in the second term at the domain D_1 is due to the factor $F(t_{n+1} | \Delta - \sum_{j=0}^n t_j)$ and it is located at the hyperplane defined as

$$\sum_{j=0}^{n+1} t_j = \Delta, \quad (26)$$

while all $F(t_k \mid \Delta - \sum_{j=0}^{k-1} t_j)$, $k = 0, \dots, n$ are continuous functions at this domain, see (9).

According to (21), the probability density $P(t_{n+1}, \dots, t_0)$ can be obtained as a sum of all I_i , $i = 0, \dots, n$ and I_{n+1} . Therefore, it inherits all the discontinuities, contained in I_i and I_{n+1} . So, at the domain D_1 , the probability density $P(t_{n+1}, \dots, t_0)$ has nonzero jump discontinuities at the $(n+2)$ hyperplanes² defined in (25) and (26), and is a continuous function at the rest of the domain.

4.6 Discontinuities in $P(t_{n+1} \mid t_n, \dots, t_0)$

Conditional probability density $P(t_{n+1} \mid t_n, \dots, t_0)$ can be easily derived from (24) according to the definition (6). It should be outlined, that joint probability density $P(t_n, \dots, t_0)$ is strictly positive for any $(n+1)$ -tuple of positive values (t_n, \dots, t_0) as it can be concluded from (24). Moreover, $P(t_n, \dots, t_0)$ is continuous at the domain

$$\sum_{i=0}^n t_i < \Delta. \quad (27)$$

Indeed, at the domain (27), we have also $\sum_{i=0}^{n-1} t_i < \Delta$, which means that the discontinuities of $P(t_n, \dots, t_0)$ are located at hyperplanes defined by conditions (25) and (26) with $(n-1)$ substituted instead of n . But those conditions are never satisfied due to (27). Thus, division of $P(t_{n+1}, \dots, t_0)$ by strictly positive and continuous function $P(t_n, \dots, t_0)$ neither does add new discontinuities, nor does it eliminate already found in the $P(t_{n+1}, \dots, t_0)$ at the domain D_1 .

Therefore, at the domain D_1 , function $P(t_{n+1} \mid t_n, \dots, t_0)$ contains $(n+2)$ jump discontinuities, located at the same positions as in $P(t_{n+1}, \dots, t_0)$, equations (25) and (26), and is a continuous function at the rest of D_1 . The location of discontinuity (26) depends on t_0 . This dependence cannot be compensated by any summands, continuous at hyperplane (26), therefore, the whole conditional probability density $P(t_{n+1} \mid t_n, \dots, t_0)$ depends on t_0 . This means, that the condition (2) does not hold for any n for the output stream of BN with delayed feedback. The Theorem 1 is proven. \square

5 Particular cases

In the previous sections, we have proven the impossibility to represent the stream of output ISI durations for BN with delayed feedback as a Markov chain of any finite order. In particular, output ISI stream is neither a sequence of independent random variables, and therefore is non-renewal, nor it is the first-order Markovian process.

In the course of proving Theorem 1, we have obtained the expression for $P(t_{n+1}, t_n, \dots, t_0)$ at the domain $\sum_{i=0}^n t_i < \Delta$ in general case of an arbitrary n , see (24). This allows to calculate the conditional probability density $P(t_{n+1} \mid t_n, \dots, t_0)$ for $\sum_{i=0}^n t_i < \Delta$ and $n = 0, 1, \dots$

In this section, we consider two particular cases of $P(t_{n+1} \mid t_n, \dots, t_0)$ when $n = 0$ and $n = 1$, namely, the single-ISI conditional probability density $P(t_1 \mid t_0)$ and the double-ISI conditional probability density $P(t_2 \mid t_1, t_0)$ and obtain the

²Note, that all hyperplanes, defined in (25) and (26) are different.

expressions for $P(t_1 | t_0)$ and $P(t_2 | t_1, t_0)$ for domain (18), as well as for all other possible domains, which were omitted in calculations with arbitrary n .

5.1 Conditional probability density $P(t_1 | t_0)$

In order to derive the exact expression for conditional probability density $P(t_1 | t_0)$ for neighbouring ISI durations, we take Steps 1–3, outlined in Section 4.1, for $n = 0$. In the case of $P(t_1 | t_0)$, there are only two domains, on which the expressions should be obtained separately, namely cases $t_0 < \Delta$ and $t_0 \geq \Delta$. Performing integration in (7), one obtains the following expressions for $P(t_1, t_0)$ at these domains:

$$\begin{aligned} P(t_1, t_0) &= F(t_1 | \Delta)P(t_0), & t_0 \geq \Delta, \\ &= F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0)g(s_0)ds_0 \\ &\quad + \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0)F(t_0 | s_0)f(s_0)ds_0, & t_0 < \Delta. \end{aligned} \quad (28)$$

Expressions (28) can be understood as follows. Since $t_0 \geq \Delta$, one can be sure that the line has time to get free from impulse during t_0 , therefore at the moment of next firing (at the beginning of t_1) the impulse enters the line and has time to live equal Δ . In the case of $t_0 < \Delta$, see (28), two possibilities arise. The first term corresponds to the scenario, when the feedback line discharges conveyed impulse within time interval t_0 , and the second one represents the case when at the beginning of t_1 the line still keeps the same impulse as at the beginning of t_0 .

Then, using (6) and (11), one obtains:

$$\begin{aligned} P(t_1 | t_0) &= F(t_1 | \Delta), & t_0 \geq \Delta, \\ &= \frac{1}{P(t_0)} \left(F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0)g(s_0)ds_0 + aF(t_1 | \Delta - t_0)F(t_0 | \Delta) \right. \\ &\quad \left. + \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0)F(t_0 | s_0)g(s_0)ds_0 \right), & t_0 < \Delta. \end{aligned} \quad (29)$$

It should be outlined, that the output ISI probability density $P(t_0)$ is strictly positive and continuous function at the domain $0 < t_0 < \Delta$. Indeed, due to (9)–(12), the only discontinuity contained in $P(t_0)$ is placed at $t_0 = \Delta$, see Figure 2 (a).

It can be shown, that the following normalization conditions take place:

$$\int_0^{\infty} dt_1 P(t_1 | t_0) = 1, \text{ and } \int_0^{\infty} dt_0 P(t_1, t_0) = P(t_1).$$

Using (9) and (29), one obtains the positions of discontinuities in $P(t_1 | t_0)$:

$$t_1 = \Delta, \quad \text{if } t_0 \geq \Delta, \quad (30)$$

$$t_1 = \Delta, \quad t_0 + t_1 = \Delta, \quad \text{if } t_0 < \Delta. \quad (31)$$

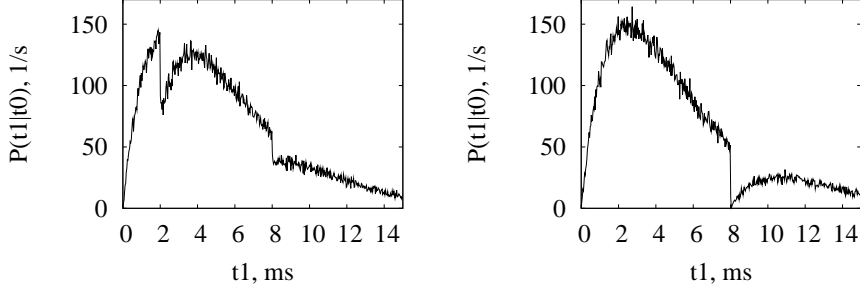


Figure 3: Conditional probability density $P(t_1 | t_0)$ for $\tau = 10$ ms, $\Delta = 8$ ms, $\lambda = 400$ s $^{-1}$, $N_0 = 2$, $t_0 = 6$ ms (left) and $t_0 = 11$ ms (right), found numerically by means of Monte-Carlo method (the number of firings accounted $N = 150\,000$).

Obviously, expressions (31) could be obtained directly from (25) and (26) by substituting $n = 0$.

As it can be seen from (30) and (31), the number of jump discontinuities in $P(t_1 | t_0)$ and their positions depend on t_0 . Therefore, the conditional probability density $P(t_1 | t_0)$ cannot be reduced to output ISI probability density $P(t_1)$. Therefore, the neighbouring output ISIs of BN with delayed feedback are correlated, as expected.

Examples of $P(t_1 | t_0)$, found for two domains numerically, by means of Monte-Carlo method (see Section 6 for details), are placed at Figure 3.

5.2 Conditional probability density $P(t_2 | t_1, t_0)$

In order to derive the exact expression for conditional probability density $P(t_2 | t_1, t_0)$ for the successive ISI durations, we take Steps 1–3, outlined in Section 4.1, for $n = 1$. In the case of $P(t_2, t_1, t_0)$, there are five domains, on which the expressions should be obtained separately, namely, the domain

$$D_1 = \{(t_0, t_1, t_2) \mid t_1 + t_0 < \Delta\},$$

which was already utilized in Section 4, and the four remaining:

$$\begin{aligned} D_2 &= \{(t_0, t_1, t_2) \mid t_0 \geq \Delta \text{ and } t_1 \geq \Delta\}, \\ D_3 &= \{(t_0, t_1, t_2) \mid t_0 < \Delta \text{ and } t_1 \geq \Delta\}, \\ D_4 &= \{(t_0, t_1, t_2) \mid t_0 \geq \Delta \text{ and } t_1 < \Delta\}, \\ D_5 &= \{(t_0, t_1, t_2) \mid t_0 < \Delta \text{ and } \Delta - t_0 \leq t_1 < \Delta\}, \end{aligned}$$

Expressions for $P(t_2 | t_1, t_0)$ can be found exactly on each domain:

$$\begin{aligned} P(t_2 | t_1, t_0) &= F(t_2 | \Delta), & (t_0, t_1, t_2) \in D_2, \\ &= F(t_2 | \Delta) & (t_0, t_1, t_2) \in D_3, \\ &= F(t_2 | \Delta - t_1), & (t_0, t_1, t_2) \in D_4, \end{aligned}$$

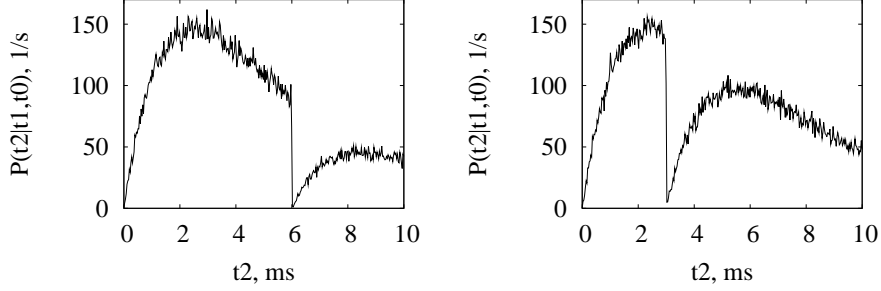


Figure 4: Conditional probability density $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 6$ ms, $\lambda = 400$ s $^{-1}$, $N_0 = 2$, $t_1=8$ ms, $t_0=8$ ms (left) and $t_1 = 3$ ms, $t_0 = 8$ ms (right), found numerically by means of Monte-Carlo method ($N = 150\,000$).

$$\begin{aligned}
&= \frac{1}{P(t_1, t_0)} \left(F(t_2 | \Delta - t_1) F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) g(s_0) ds_0 \right. \\
&+ F(t_2 | \Delta) \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0) F(t_0 | s_0) g(s_0) ds_0 + a F(t_2 | \Delta) F(t_1 | \Delta - t_0) F(t_0 | \Delta) \Big), \\
&\hspace{15em} (t_0, t_1, t_2) \in D_5, \\
&= \frac{1}{P(t_1, t_0)} \left(F(t_2 | \Delta - t_1) F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) g(s_0) ds_0 \right. \\
&+ F(t_2 | \Delta) \int_{t_0}^{t_0+t_1} F(t_1 | s_0 - t_0) F(t_0 | s_0) g(s_0) ds_0 \\
&+ \int_{t_0+t_1}^{\Delta} F(t_2 | s_0 - t_0 - t_1) F(t_1 | s_0 - t_0) F(t_0 | s_0) g(s_0) ds_0 \\
&+ a F(t_2 | \Delta - t_0 - t_1) F(t_1 | \Delta - t_0) F(t_0 | \Delta) \Big), \hspace{1em} (t_0, t_1, t_2) \in D_1. \quad (32)
\end{aligned}$$

where $P(t_1, t_0) = F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) g(s_0) ds_0 + \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0$, according to (29).

It is worth to notice, that $P(t_1, t_0)$ is strictly positive and continuous function on both D_1 and D_5 , see denominators in (32). Indeed, from (30) and (31) one can see, that $P(t_1, t_0)$ may include discontinuities only at the points $t_1 = \Delta$ and $t_1 = \Delta - t_0$. None of these points fall into D_1 , or D_5 .

It can be shown, that the following normalization conditions take place:

$$\int_0^{\infty} dt_2 P(t_2 | t_1, t_0) = 1, \text{ and } \int_0^{\infty} dt_0 P(t_0, t_1, t_2) = P(t_2, t_1).$$

Using (9) and (32), one derives the positions of jump discontinuities in the conditional probability density $P(t_2 | t_1, t_0)$:

$$t_2 = \Delta, \hspace{15em} (t_0, t_1, t_2) \in D_2 \cup D_3, \quad (33)$$

$$t_1 + t_2 = \Delta, \hspace{15em} (t_0, t_1, t_2) \in D_4. \quad (34)$$

$$t_2 = \Delta, \quad t_1 + t_2 = \Delta \hspace{15em} (t_0, t_1, t_2) \in D_5, \quad (35)$$

$$t_2 = \Delta, \quad t_1 + t_2 = \Delta, \quad t_0 + t_1 + t_2 = \Delta, \hspace{1em} (t_0, t_1, t_2) \in D_1. \quad (36)$$

Obviously, expression (36) could be obtained directly from (25) and (26) by

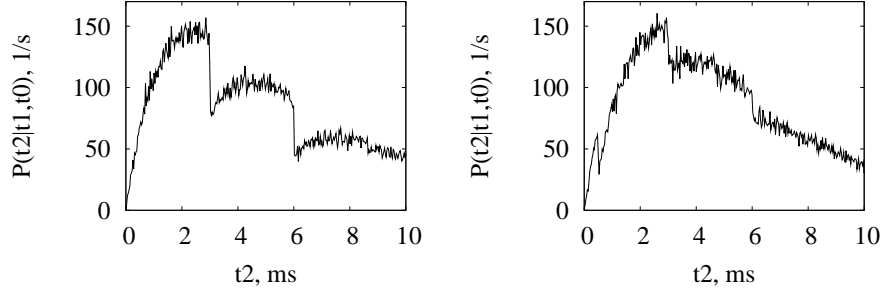


Figure 5: Conditional probability density $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 6$ ms, $\lambda = 400$ s $^{-1}$, $N_0 = 2$, $t_1=3$ ms, $t_0=3.5$ ms (left) and $t_1 = 3$ ms, $t_0 = 2.5$ ms (right), found numerically by means of Monte-Carlo method ($N = 150\,000$).

substituting $n = 1$.

As one can see, the number and the position of jump discontinuities in $P(t_2 | t_1, t_0)$ depends on t_0 , therefore $P(t_2 | t_1, t_0)$ cannot be reduced to $P(t_2 | t_1)$, which means that the output stream is not first-order Markovian.

Examples of $P(t_2 | t_1, t_0)$, found numerically for different domains, are placed at Figures 4 and 5.

6 Numerical simulation

In order to check the correctness of obtained analytic expressions, and also to investigate whether the output ISIs stream is non-Markovian for inhibitory BN with higher thresholds as well as for $N_0 = 2$, numerical simulations were performed. A C++ program, containing class, which models the operation manner of inhibitory BN with delayed feedback, was developed. Object of this class receives the sequence of pseudorandom numbers with Poisson probability density to its input. The required sequences were generated by means of utilities from the GNU Scientific Library³ with the Mersenne Twister generator as source of pseudorandom numbers.

Program contains function, the time engine, which brings system to the moment just before the next input signal, bypassing moments, when neither external Poisson impulse, nor impulse from the feedback line comes. So, only the essential events are accounted. It allows one to make exact calculations faster as compared to the algorithm where time advances gradually by adding small time-steps.

The conditional probability densities, $P(t_1 | t_0)$ and $P(t_2 | t_1, t_0)$, are found by counting the number of output ISI of different durations and normalization (see Figures 3 – 6). Obviously, for calculation of conditional distributions only those ISIs are selected, which follow one or two ISIs of fixed duration, t_0 for $P(t_1 | t_0)$ and $\{t_1, t_0\}$ for $P(t_2 | t_1, t_0)$. The number and the positions of discontinuities, obtained in numerical experiments for inhibitory BN with threshold 2, coincide with those predicted analytically in (30), (31) and (33) – (36).

³<http://www.gnu.org/software/gsl/>

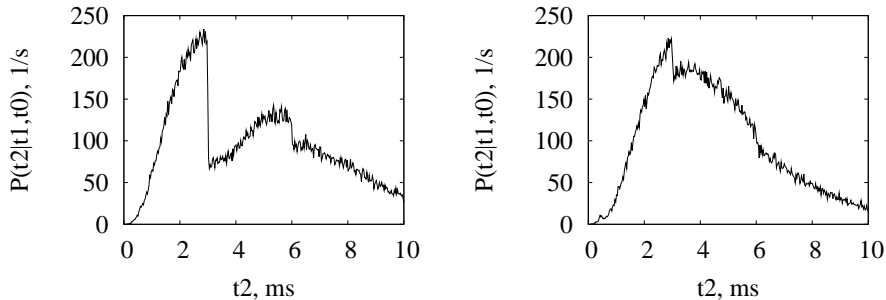


Figure 6: Conditional probability density $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 6$ ms, $\lambda = 1000$ s $^{-1}$, $N_0 = 4$, $t_1 = 3$ ms, $t_0 = 3.5$ ms (a) and $t_1 = 3$ ms, $t_0 = 2.5$ ms (b), found numerically by means of Monte-Carlo method ($N = 150\,000$).

For $N_0 > 2$, conditional probability densities $P(t_1 | t_0)$ and $P(t_2 | t_1, t_0)$ are similar to those, found for $N_0 = 2$. In particular, both the quantity and position of discontinuities coincide with those obtained for inhibitory BN with threshold 2, as expected, compare Figures 6 and 5.

7 Conclusions and discussion

Our results reveal the influence of delayed feedback presence on the neuronal firing statistics. In the contrast to the cases of BN without feedback [36] and BN with instantaneous feedback [37], the neighbouring output ISIs of inhibitory BN with delayed feedback are mutually correlated. This means that even in the simplest possible recurrent network the output ISI stream cannot be treated as a renewal one.

The non-renewalness of experimentally registered spike trains was observed for neuronal activity in various CNS areas in mammals [5, 38, 39] and fish [6, 7]. The simplest stochastic processes which are not renewal are the Markov processes of various order. The order of underlying Markov process was estimated in [7] for activity in the weakly electric fish electrosensory system. It was found in [7] that for some neural fibers the Markov order should be at list seven, which does not exclude that the genuine order is higher, or that the activity is non-Markovian.

Actually, for proving based on experimental data that a stochastic activity has Markov order m , one needs increasing amount of data with increasing m . If so, it seems impossible to prove experimentally that a stochastic activity is non-Markovian. Similarly as it is impossible to prove experimentally that a number is irrational. We prove here that the output ISI stream of inhibitory BN with delayed feedback is non-Markovian based on complete knowledge of the mechanism which generates the output stream. In a sense, to have this knowledge is equivalent as to have an unlimited amount of experimental data.

It is worth to notice, that the activity of excitatory BN with delayed feedback is non-Markovian as well [40]. We conclude, that it is namely the delayed feedback presence, which results in non-Markovian statistics of neuronal firing. One should take this facts into account during analysis of neuronal spike trains

obtained from any recurrent network.

A Proof of Lemma 1

In the compound event (t_{n+1}, s_{n+1}) , the time to live s_{n+1} always gets its value before than the t_{n+1} does. The value of s_{n+1} can be determined unambiguously from the (t_n, s_n) value (See Sections 2.2 and 4.3):

$$\begin{aligned} s_{n+1} &= s_n - t_n, & t_n < s_n, \\ &= \Delta, & t_n \geq s_n. \end{aligned}$$

The only two factors, which determine the next ISI duration, t_{n+1} , are (i) the value of s_{n+1} , and (ii) the behavior of the input Poisson stream under the condition $(t_n, s_n; \dots; t_0, s_0)$ after the moment θ , when the t_{n+1} starts. The s_{n+1} value does not depend on $(t_{n-1}, s_{n-1}; \dots; t_0, s_0)$, see above. As regards the input Poisson stream, condition $(t_n, s_n; \dots; t_0, s_0)$ imposes certain constraints on its behavior before the θ . Namely, if $t_i \neq s_i$ for some $0 \leq i \leq n$, than one can conclude that an input impulse was obtained just at the end of t_i . In the opposite situation, when $t_i = s_i$, one can conclude that in the course of t_i exactly one impulse was obtained from the Poisson stream. But what do we need in the definition of the $P(t_{n+1}, s_{n+1} | t_n, s_n; \dots; t_0, s_0)$, it is the conditional probability to obtain input impulses at definite moments after the θ . For a Poisson stream this conditional probability does not depend on conditions before the θ . For example, conditional probability to obtain the first after θ impulse at $\theta + t$ equals $e^{-\lambda t} \lambda dt$, whatever conditions are imposed on the stream before the θ . This proves (3). \square

B Finding integrals I_i for $P(t_{n+1}, \dots, t_0)$

Domain of s_0 values covered by I_i , $i = 0, \dots, n$, corresponds to the scenario, when impulse, which was in the feedback line at the beginning of interval t_0 (with time to live s_0), will reach BN during interval t_i , see Figure 7. In this process, after each firing, which starts ISI t_k , $k \leq i$, the time to live of the impulse in the feedback line is decreased exactly by t_{k-1} . This means, that variables of integration $\{s_0, \dots, s_{n+1}\}$, above, are not actually independent, but must satisfy the following relations:

$$s_k = s_0 - \sum_{j=0}^{k-1} t_j, \quad k = 1, \dots, i, \quad (37)$$

which are also ensured by δ -function in the bottom line of (17). Next to s_i time to live must be equal Δ :

$$s_{i+1} = \Delta, \quad (38)$$

and this is ensured by δ -function in the top line of (17).

The next to s_{i+1} times to live again are decreased by corresponding ISI with each triggering. Due to (18), this brings about another set of relations:

$$s_k = \Delta - \sum_{j=i+1}^{k-1} t_j, \quad k = i+2, \dots, n+1, \quad (39)$$

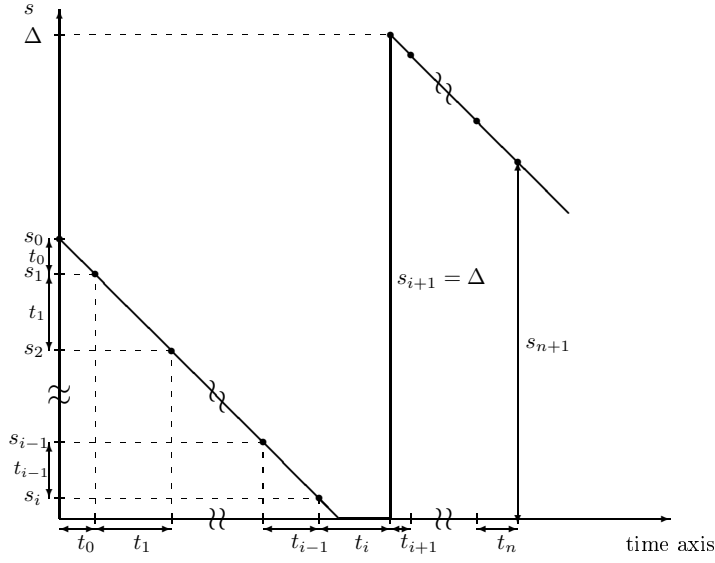


Figure 7: Illustration of relations between (t_0, \dots, t_n) and (s_0, \dots, s_{n+1}) contributing to the I_i : $s_0 \in] \sum_{j=0}^{i-1} t_j; \sum_{j=0}^i t_j]$, $\sum_{j=0}^n t_j < \Delta$. The time to live s_k decreases steadily with every output firing for $k = 0, \dots, i - 1$ until it becomes that $s_i < t_i$. Then, during the time interval t_i the line discharges its impulse to BN input, and at the beginning of t_{i+1} starts to convey the new one with time to live $s_{i+1} = \Delta$. After that, times to live s_k are again decreased by corresponding t_k with each firing, $k = i + 1, \dots, n$.

which are again ensured by δ -function in the bottom line of (17). Relations (37), (38) and (39) together with limits of integration over s_0 in (19) ensure that at D_1 the following inequalities hold:

$$\begin{aligned} s_k &> t_k, & k = 0, \dots, i-1, \\ s_i &\leq t_i, \\ s_k &> t_k, & k = i+1, \dots, n. \end{aligned} \quad (40)$$

Inequalities (40) allow one to decide correctly which part of rhs of (17) should replace each transition probability $P(t_k, s_k | t_{k-1}, s_{k-1})$ in (19), and perform all but one integration. This gives:

$$\begin{aligned} I_i &= \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} \\ &\quad F(t_0 | s_0) f(s_0) \prod_{k=1}^i F(t_k | s_k) \delta(s_k - s_0 + \sum_{j=0}^{k-1} t_j) \\ &\quad \times F(t_{i+1} | s_{i+1}) \delta(s_{i+1} - \Delta) \prod_{k=i+2}^{n+1} F(t_k | s_k) \delta(s_k - \Delta + \sum_{j=i+1}^{k-1} t_j) \\ &= \prod_{k=i+1}^{n+1} F(t_k | \Delta - \sum_{j=i+1}^{k-1} t_j) \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} \prod_{k=0}^i F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) g(s_0) ds_0, \\ &\quad i = 0, 1, 2, \dots, n. \end{aligned} \quad (41)$$

The last expression might be obtained as well by means of consecutive substitution of either top, or bottom line of (17) into (19), without previously discovering (37) – (40).

Finally, integral I_{n+1} corresponds to the case, when at the beginning of interval t_{n+1} , the line still keeps the same impulse as at the beginning of t_0 . Therefore, I_{n+1} comprises the rest of scenarios contributing to the value of $P(t_{n+1}, \dots, t_0)$ in (5). Proceeding as in the preceding terms, the contribution I_{i+1} reads:

$$\begin{aligned} I_{n+1} &= \int_{\sum_{j=0}^n t_j}^\Delta ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} \\ &\quad F(t_0 | s_0) f(s_0) \prod_{k=1}^{n+1} F(t_k | s_k) \delta(s_k - s_0 + \sum_{j=0}^{k-1} t_j) \\ &= \int_{\sum_{j=0}^n t_j}^\Delta \prod_{k=0}^{n+1} F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) f(s_0) ds_0 \\ &= \int_{\sum_{j=0}^n t_j}^\Delta \prod_{k=0}^{n+1} F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) g(s_0) ds_0 + a \prod_{k=0}^{n+1} F(t_k | \Delta - \sum_{j=0}^{k-1} t_j). \end{aligned} \quad (42)$$

C Continuity of integral factor in (22)

Continuity in D_1 of the integral factor

$$\int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} \prod_{k=0}^i F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) g(s_0) ds_0, \quad i = 0, 1, \dots, n, \quad (43)$$

in the expression (22) can be proven after mathematical simplification. First, notice that due to integration domain the following inequalities take place

$$s_0 - \sum_{j=0}^{k-1} t_j > t_k, \quad k = 0, 1, \dots, i-1, \quad s_0 - \sum_{j=0}^{i-1} t_j < t_i,$$

which together with (9) allows to replace (43) with the following

$$\prod_{k=0}^{i-1} (\lambda^2 t_k e^{-\lambda t_k}) \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} (1 + \lambda s_1) e^{-\lambda s_1} P^0(t_i - s_1) g(s_0) ds_0,$$

where $s_1 = s_0 - \sum_{j=0}^{i-1} t_j$. The continuity of the last expression is determined by the continuity of its second factor, since the first one is continuous in \mathbb{R}^{n+2} . The second factor can be replaced with

$$\int_0^{t_i} (1 + \lambda s_0) e^{-\lambda s_0} P^0(t_i - s_0) g\left(s_0 + \sum_{j=0}^{i-1} t_j\right) ds_0. \quad (44)$$

after changing the variable of integration. For further simplification of the last expression use (1), (18) and (10), which gives instead of (44)

$$\begin{aligned} & \int_0^{t_i} (1 + \lambda s_0) e^{-\lambda s_0} \lambda^2 (t_i - s_0) e^{-\lambda(t_i - s_0)} g\left(s_0 + \sum_{j=0}^{i-1} t_j\right) ds_0 = \\ & = e^{-\lambda t_i} \int_0^{t_i} (1 + \lambda s_0) \lambda^2 g\left(s_0 + \sum_{j=0}^{i-1} t_j\right) ds_0 - \end{aligned} \quad (45)$$

$$- e^{-\lambda t_i} \int_0^{t_i} (1 + \lambda s_0) \lambda^2 s_0 g\left(s_0 + \sum_{j=0}^{i-1} t_j\right) ds_0. \quad (46)$$

The required continuity of (43) is determined by the continuity of integral factors in (45) and (46). Now, take into account the explicit expression for $g(s)$, which is found in [34, Eq. (15)]. For our purposes it is enough to know that $g(s) = A + B e^{2\lambda s}$, where A and B are constants. Taking this into account, the integral factor in (45) can be replaced with

$$A \int_0^{t_i} (1 + \lambda s_0) \lambda^2 ds_0 + B e^{2\lambda \sum_{j=0}^{i-1} t_j} \int_0^{t_i} (1 + \lambda s_0) \lambda^2 e^{2\lambda s_0} ds_0,$$

which makes its continuity self-evident. The same is for integral factor in (46).

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